Recruitment Patterns in a Mediterranean Oak Forest: A Case Study Showing the Importance of the Spatial Component

Sara Maltez-Mouro, Luis V. García, Teodoro Marañón, and Helena Freitas

Abstract: The spatial patterns of recruits in a Mediterranean forest in Southwest Portugal were examined. We aimed to investigate how several environmental and canopy variables contribute to the observed patterns, and how relevant the spatial component is in explaining the variance in the density of recruits. We took a census of every recruit of four dominant woody species (*Arbutus unedo*, *Quercus faginea*, *Q. suber*, and *Viburnum tinus*), mapping their position inside two forest plots. For a total of 309 recruits, we measured the following variables: soil moisture, slope, canopy density, herbaceous and litter ground cover, overlying species and height, and distance to the nearest adult of the same and different species. Spatial pattern analysis, principal coordinate analysis of neighbor matrices, canonical correspondence analysis, and variance partitioning were performed to detect significant deviations from complete spatial randomness and identify conspecific and interspecific patterns, characterize regeneration niches, and evaluate the importance of the spatial component. Results showed the existence of significant community structure at the recruitment stage. The distance between recruits and the nearest conspecific adult was the main explanatory variable. Light availability, soil moisture, litter accumulation, and the overlying species were also significant factors in explaining the variance in the density of recruits. The best model accounted for 37% of the overall variance in the density of recruits, and most (80%) of the explained variance corresponded to spatially structured variance. This case study shows the importance of the spatial component in understanding the forest regeneration patterns under Mediterranean conditions and will contribute to the implementation of ecologically based management actions to preserve the remaining forest fragments. FOR. SCI. 53(6):645–652.

Keywords: J function, principal coordinate analysis of neighbor matrices (PCNM), *Quercus faginea*, *Quercus suber*, variance partitioning

SPATIAL PATTERNS play a key role in ecosystem dynamics and constitute a kind of "ecological fingerprint" that characterizes the essential processes and structures of a system (Goreaud and Pélissier 2003). Knowing the spatial patterns of organisms is useful in identifying particular mechanisms, in explaining the ecosystem functioning and stability, and in designing adequate management, recovery, or restoration actions (Miller et al. 2002, Maestre et al. 2005).

Many studies have focused on spatial distributions of tree species, on positive or negative spatial associations between species and between size classes, and on the spatial patterns of tree recruitment in temperate, boreal, or tropical forests (e.g., Dovciak et al. 2001, Gratzer and Rai 2004, García and Houle 2005). However, few studies of that type have been conducted in Mediterranean forests or focused on very fine-scale (<1 m^2) patterns of regenerating Mediterranean woody species. For example, Gómez-Aparicio et al. (2005) demonstrated that the modification of the abiotic environment by shrubs benefited seedling establishment of *Quercus ilex* and *Q. pyrenaica*; however, at the microsite scale (i.e., within habitat heterogeneity), neither light nor soil compaction predicted variations in seedling fate. Maestre et al. (2003) demonstrated the role of small-scale heterogeneity of soil surface properties in providing safe sites for seedling establishment of *Pistacia lentiscus* in semiarid conditions, where the spatial structure of the environmental variables represented 17–40% of the explained variation in seedling survival.

The spatial patterns of successfully established plant species depend on a chain of processes, including dispersal patterns, germination and emergence responses, and seedling growth and survival (Herrera et al. 1994, Jordano and Herrera 1995). However, the regeneration requirements (regeneration niche) of each species can be inferred from the microenvironmental variables associated with the successful saplings and juveniles (Marañón et al. 2004).

It is particularly important to increase our knowledge of the regeneration requirements of coexisting woody species within Mediterranean forests of the southwestern Iberian

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Peninsula (Marañón et al. 2004). Historically, natural forests throughout the Mediterranean Basin have been disturbed or destroyed by human activities, and today only a fragmented pattern, representing 9–10% of the area, remains (Marchand 1990). These locally rare forest ecosystems need the implementation of ecologically based management actions to guarantee their restoration and conservation and to prevent the loss of biodiversity.

In this case study we investigate the recruitment spatial patterns of the main woody species that regenerate in a mixed-oak Mediterranean forest in southern Portugal. We illustrate how general ecological concepts and knowledge about spatial patterns in other forests apply to these locally rare and fragmented ecosystems and contribute to improving general knowledge of this type of natural forest. First, we analyze how several environmental variables relate to the observed spatial patterns of recruits. Furthermore, we investigate the role of the overstory structure and composition in the observed recruitment patterns, because the physical environment perceived by seeds, seedlings, and recruits is highly modified by the already established individuals (George and Bazzaz 1999). Finally, we evaluate the importance of the spatial structure in explaining the distribution of recruits. We also prove the usefulness of applying novel techniques for handling the spatial component, in particular, the variance partitioning, together with principal coordinate analysis of neighbor matrices (PCNM) (Borcard and Legendre 2002, Dray et al. 2006).

Methods

Study Site

The study site is located in the Sudoeste Alentejano e Costa Vicentina Natural Park, SW Portugal (37°40′N, 8°43′W). The climate is Mediterranean, with mild wet winters and warm dry summers. The mean annual precipitation is ~600 mm, with only 10% occurring between May and September, and the mean annual temperature is ~15°C, with mean maximum and minimum annual temperatures of ~29 and 6°C, respectively (PNSACV 2002).

The study site is on a north-facing slope (32°) within a mixed-oak forest composed of evergreen oaks (cork oak, *Quercus suber* L.) and deciduous oaks ("carvalho-cerquinho," *Q. faginea* Lam.). Other dominant woody species are the strawberry tree (*Arbutus unedo* L.) and the laurestine (*Viburnum tinus* L.) (Maltez-Mouro et al. 2005).

The main bedrock is greywacke, and soils are acidic (mean pH = 5.0) and low in nutrients (especially in N and P) (Maltez-Mouro et al. 2005). The forest is relatively well preserved, and there is no record of fire or logging since at least 1956. Management is limited to the periodic (at approximately 9-year intervals) removal of the bark from the largest cork oak trees for cork production.

Study Species

Four dominant woody species were studied: *A. unedo*, *Q. faginea*, *Q. suber*, and *V. tinus*. Both species of *Quercus* occur only in the Mediterranean Basin and frequently exhibit lack of regeneration (e.g., Pérez-Ramos 2007). They disperse their seeds mainly by gravity near the mother tree and also sprout from roots and produce vegetative saplings that are difficult to distinguish from old seedlings. A small fraction of the seeds can be dispersed short distances by rodents (Pulido and Díaz 2005) or long distances by birds (*Garrulus glandarius*) (Gómez 2003), with important ecological and genetic consequences.

A. unedo is a small evergreen tree widely distributed in the Mediterranean region. Its abundance and ecological importance have increased in the Mediterranean region, because it occupies disturbed forests, sometimes being the only arborescent species in shrublands that substitute natural oak forests. Although it can sprout readily from the base, reproduction and colonization of new sites are entirely by seeds (Sealy and Webb 1950). It produces large fleshy berries (10–20 mm) bearing 20–40 tiny seeds (2–3 mm) dispersed by birds.

V. tinus is an evergreen arborescent shrub typical of native Mediterranean forests. Adult plants produce a high number of fruits, which are eaten by birds, and the seeds are dispersed under trees or shrubs. Juvenile plants are able to persist in the shaded and dry forest understory for a long time by a combination of mechanisms that reduce the demand for resources and enhance the capture of resources (Sack et al. 2003).

Sampling Methods

We established two 32 × 10 m plots within the forest site: one on the lower forest slope (hereafter plot D) dominated by *Q. faginea* and the other on the upper slope (plot U), dominated by *Q. suber*. Although further replication would be desirable, the detailed inspection of fine-scale (<1 m) spatial structure and microenvironmental conditions is time-consuming. In the trade-off between the number of plots and the level of detail, we opted for increasing the detail (and replication) at the individual level (i.e., each recruit of four species), rather than replication at the plot level.

We took a census of every recruit of *A. unedo*, *Q. faginea*, *Q. suber,* and *V. tinus*. For *Quercus*, these included seedlings as well as some vegetative recruits from roots, whereas recruits of *A. unedo* and *V. tinus* were mostly seedlings. All were designated as recruits for simplification.

Each individual recruit between 10 and 130 cm tall was mapped (with a precision of 1 cm) using tape measures after subdividing each plot into 16 quadrats of 4 × 5 m. Plastic rings of 50-cm diameter were centered on each recruit, and the following environmental variables were measured either on the forest floor inside them or within a vertical cylinder above them: soil moisture (% volume, using time domain reflectometry); slope (degrees, using a clinometer positioned on the floor); overstory canopy density (%, using a spherical densitometer positioned 1 m above the ground); ground cover of perennial herbaceous plants and litter (%, by direct visual estimation at increments of 5%), litter depth (cm); overlying species over each recruit (or, in some cases, the occurrence of canopy gaps); maximum overstory canopy height (height classes 2–4, 4–6, and >6 m); density of overstory canopy layers (counting one layer per each height

class); distance to the nearest conspecific adult; and distance to the nearest adult of a different species (considering as an adult every plant able to reproduce).

The density of recruits (number of recruits per unit area) corresponds to the intensity of the point process subject to spatial pattern analysis. The number of neighbors was further calculated for each individual recruit, counting all recruits within a radius of 1 m from each focal recruit. The percent cover of each overstory species was calculated from the total number of occurrences of each canopy species over all species recruits in each plot.

Data Analysis

To investigate the recruitment spatial pattern at the community level, we first studied the overall dispersion of all individuals, irrespective of the species. Second, we analyzed the conspecific (univariate) spatial pattern. Finally, we investigated the pattern of each recruit species relative to the seedlings of the remaining species, i.e., the interspecific (multivariate) associations.

To analyze the overall spatial patterns, we used the modified Ripley's K function, $L(r) = r - \sqrt{(K(r)/pi)}$, which makes interpretation easier (Diggle 2003); when $L(r)$ is plotted against distance (r), negative values indicate clumping, and positive values indicate overdispersion (Fortin and Dale 2005). For analyzing the conspecific associations, we used the J function, which combines the nearest neighbor distance distribution function ($G(r)$) and the empty space function ($F(r)$) by simply taking the ratio $J(r) = (1 - G(r))/(1 - F(r))$ (Baddeley and Turner 2005). The *J* function has many advantages over isolated F or G functions (Thönnes and van Lieshout 1999, Baddeley et al. 2000), and it is equal to 1 for a completely random (uniform Poisson) point process, while deviations $J(r) < 1$ or $J(r) > 1$ indicate spatial clumping or spatial overdispersion, respectively (van Lieshout 2004, Baddeley and Turner 2005). For interspecific multivariate analysis, we used the "type *i* to any type" multitype J function (Baddeley and Turner 2005). For K function, an edge correction was applied using the "isotropic" method (Baddeley and Turner 2005), whereas for the J function the uncorrected estimates can be used and directly interpreted without edge correction (Thönnes and van Lieshout 1999, Baddeley et al. 2000). All statistics used in this study go beyond simple testing for overall pattern, providing a detailed description of spatial structure (Moeur 1993).

Using Monte Carlo simulations, estimates of $K*(r)$ or $J*(r)$ were computed and 99% confidence envelopes were created for comparison with the estimated empirical function. Clear identification of the null hypotheses was important to avoid erroneous interpretations of the spatial structure and wrong biological conclusions (Goreaud and Pélissier 2003). The hypothesis of complete spatial randomness (CSR) was the null hypothesis tested against the statistics of univariate patterns. The hypothesis of independence between species was the null hypothesis tested against statistics used for multispecies patterns; i.e., statistics were tested conditionally on the spatial pattern of each species, keeping the location of one species unchanged and shifting the points of the other species by a random vector, considering the study area as a torus (Goreaud and Pélissier 2003, Baddeley and Turner 2005).

Canonical correspondence analysis (CCA) (ter Braak 1986) was performed to study the relationships between the environmental variables and the recruitment patterns of the species studied. The response matrix corresponds to the dummy variables representing the species of each recruit, but all the theory of CCA applies equally (ter Braak and Smilauer 2002, p. 61). Manual selection and Monte Carlo permutation tests (with 9,999 unrestricted permutations) under the full model were used for selecting the most significant variables from the explanatory set and to evaluate the significance of the extracted axes. The stepwise option was used to exclude highly redundant independent variables and to accurately detect the best predictors in the model (Økland and Eilertsen 1994, Vandvik and Birks 2002).

To explicitly introduce and remove the spatial component in the model, we used PCNM (Borcard and Legendre 2002, Dray et al. 2006). This method basically consists of diagonalizing a spatial weighting matrix and then extracting the eigenvectors that maximize Moran's autocorrelation index (Dray et al. 2006). These eigenvectors can be used directly as spatial predictors or as covariables in CCA or in partial CCA analysis (Økland and Eilertsen 1994, Dray et al. 2006). Variance partitioning (Borcard et al. 1992) was accomplished to remove the spatial correlation between individuals, to determine how important the spatial component itself is in explaining the distribution and associations of the recruits, and to ascertain what fraction of the spatial structure of the recruits results from their dependence on the measured environmental variables. The independence between the species of recruits in the understory and the species in the overstory was tested using the χ^2 test (degrees of freedom equals 32 for each forest plot and 40 when the two plots were considered together).

Significance was fixed at the 0.05 level throughout the study. Because repeated tests were performed, type I error inflation was controlled by applying a sequential Bonferroni procedure (see García 2004). Data were processed using CANOCO for Windows, version 4.5 (ter Braak and Smilauer 2002), the Spatstat package (Baddeley and Turner 2005) for R (R Development Core Team 2006), and the SpaceMaker2 program (Borcard and Legendre 2004).

Results

A total of 309 recruits were recorded, and their spatial locations in the forest plots are shown in Figure 1. Average recruitment density was 0.557 recruits/m^2 in the upper plot (U) and 0.436 recruits/m^2 in the lower plot (D). The arborescent shrub *V. tinus* had the highest recruitment density in both plots, followed by *Q. suber* (in plot U) and *Q. faginea* (in plot D). In contrast, the overstory canopy layer was dominated by *Q. faginea* (51 and 38% in plots D and U, respectively) and *A. unedo* (38% in plot U) (Table 1).

Recruitment Spatial Patterns

The overall spatial pattern of recruits departed significantly from random. There was an all-species clumped

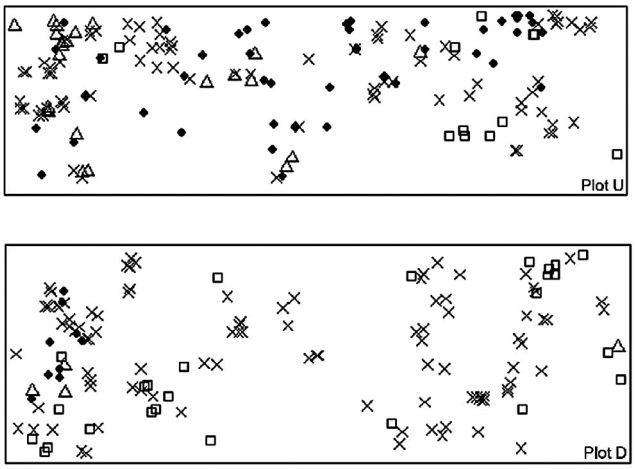

Figure 1. Spatial location of recruits of the four main species regenerating in a Mediterranean forest in South-west Portugal. Two 32 × 10 m plots: plot U, upper slope; plot D, lower slope. △, *A. unedo*; □, *Q. faginea*, ♦, *Q. suber*; and ×, *V. tinus*.

pattern, as indicated by the L(*r*) transformation of the estimated K(*r*) function clearly below the confidence envelopes for the null hypothesis of complete spatial randomness (Figure 2).

Figure 3 shows the results of point pattern analysis for conspecific (univariate) and interspecific (multivariate) spatial distributions and associations. It shows some evidence of clumped patterns (7 from 15 graphs) and CSR (8 from 15 graphs), but there were no segregation patterns. Regarding the conspecific patterns, recruits of *V. tinus* were clumped at both forest plots, whereas recruits of *Q. faginea* and *Q. suber* were clumped only in plot U or D, respectively; recruits of *A. unedo* were clumped in plot U, but this species could not be tested for plot D because of the extremely low density. Regarding the interspecific patterns, only recruits of *A. unedo*, *Q. suber*, and *V. tinus* showed slightly clumped multivariate patterns and only in the upper forest plot.

Factors Affecting Regeneration

The environmental characterization of the two forest plots is shown in Table 2 (see general description of the forest in Maltez-Mouro et al. 2005). The forest plot downslope (D), which was dominated by *Q. faginea*, had a greater amount of litter but lower herbaceous ground cover, and the overstory canopy was taller, denser, and more multilayered. Density of recruits was lower in this plot (D), and thus the average distance between recruits and the nearest adult of different species was higher. The average

Table 1. Recruitment density and relative abundance of adults in the overstory canopy layer in the two forest plots.

	Recruits (individuals/m^2)		Overstory (%)	
	Plot U	Plot D	Plot U	Plot D
A. unedo	0.0806	0.0128	38	34
Q. faginea	0.0420	0.0833	38	51
Q. suber	0.1580	0.0288	19	5
V. tinus	0.2770	0.3110	5	10
Total	0.5570	0.4360	100	100

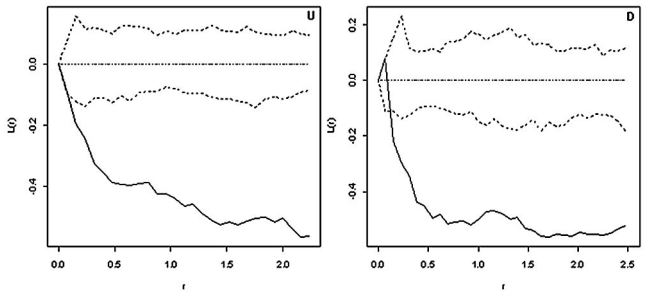

Figure 2. Modified Ripley's *K* function of the spatial distribution of recruits, in the upper (U) and lower (D) forest plots. *r* is the distance in meters (vector of distances at which the function was estimated), the horizontal line is the theoretical value of L(*r*) for a stationary Poisson process, dashed lines represent the limits of confidence envelopes (determined after Monte Carlo simulations), and the solid line is the estimated empirical function.

distance from recruits to the nearest adult of the same species followed a rank-by-species that was similar in the two plots (average distance in parentheses): *V. tinus* (348.4 cm) > *Q. suber* (227.2 cm) > *Q. faginea* (146.3 cm) > *A. unedo* (124.7 cm).

Table 3 shows results of variance partitioning. Only 22 or 21% of the explained variance in the density of recruits (for plot U or D, respectively) was nonspatially structured, whereas nearly 80% of explained variance was spatially structured in both plots. Of that spatially structured variance, less than one-third was explained by environmental variables. Therefore, most of the spatially structured variance that was explained was related to community-based processes or to nonmeasured environmental variables.

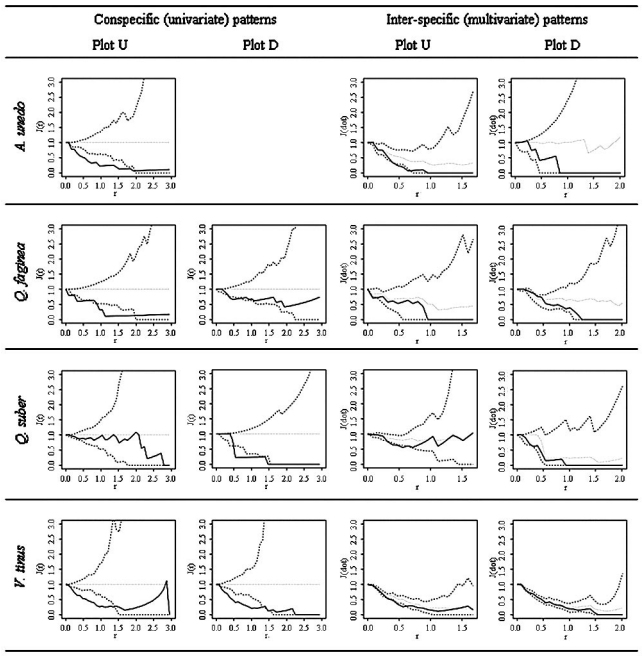

Figure 3. Results of spatial pattern analyses of species recruitment. J(*r*) is the J function and J(dot) is the "type I to any type" multitype J function, both defined by Baddeley and Turner (2005), *r* is the distance (vector of distances at which the function was estimated), the dotted line is the theoretical value of J functions for the null hypothesis, dashed lines represent the limits of confidence envelopes (determined after Monte Carlo simulations), and the solid line is the estimated empirical function. Conspecific patterns for recruits of *A. unedo* could not be calculated for plot D owing to their low density.

Table 2. Environmental characterization of the two forest plots

Variable	Plot U	Plot D
Number of neighbors	4.5 ± 2.7	3.9 ± 2.4
Canopy layers	1.3 ± 0.6	2.0 ± 0.7
Litter ground-cover (%)	63.3 ± 28.1	86.9 ± 13.0
Herbs ground-cover (%)	14.5 ± 19.3	2.8 ± 5.9
Litter depth (cm)	5.1 ± 2.3	6.1 ± 2.1
Maximum canopy height (m)	4.3 ± 1.9	5.6 ± 1.7
Distance to different species (cm)	57.2 ± 30.1	78.3 ± 43.9
Distance to same species (cm)	269.3 ± 176.9	236.5 ± 167.7
Slope (°)	31.3 ± 10.1	28.1 ± 10.1
Canopy density (%)	89.2 ± 10.5	95.8 ± 3.3
Soil moisture (m^3/m^{-3})	0.09 ± 0.02	0.08 ± 0.01

Data are means ± SD.

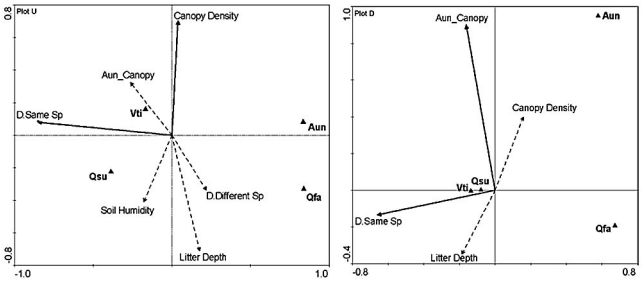

Figure 4. Plane defined by the two first axes of stepwise partial CCA of recruits constrained by environmental variables and using the best spatial predictors as covariables. Projection of the species of recruits (▲), significant environmental predictors (solid arrows), and supplementary environmental variables (dashed arrows) studied that had significant correlation with the extracted pCCA axes (after controlling the overall family-wise error rate at the 0.05 level) are shown. The graph on the left is for the upper-slope plot (U), and the graph at the right is for the lower-slope plot (D). Aun, *A. unedo*; Qfa, *Q. faginea*; Qsu, *Q. suber*; Vti, *V. tinus*; D.Same Sp. and D. Different Sp., distance between each recruit and the nearest adult of the same and different species; Aun_Canopy, presence of *A. unedo* in the overstory canopy layer.

Figure 4 shows the results of stepwise partial CCA (pCCA) of recruits constrained by environmental variables and using the best spatial predictors as covariables. One of the best explanatory variables was the distance between recruits and the nearest adult of the same species, which was negatively correlated with the first pCCA axis. For both plots, recruit density of *Q. faginea* is negatively correlated to the main axis. Therefore, in this species, recruit density tends to increase toward conspecific adults. This is also the case for *A. unedo.* In contrast, *Q. suber* and *V. tinus* seem to have their recruit density optima at larger distances from their respective conspecific adults (Figure 4). The other best explanatory variables were canopy density (for plot U) and the canopy of *A. unedo* (for plot D), both strongly correlated to the second pCCA axis. The projection of other significant environmental and canopy variables, as supplementary variables in the CCA graphs was done to improve the interpretation of the main trends. The null hypothesis of independence between species of recruits in the understory and species in the overstory was rejected (χ^2 test [40, 0.05], $P = 0.00004$).

Discussion

Species Regeneration Ecology

In the forest studied, the relative abundance of each species as adults in the overstory differs from that in the recruitment stage. For example, *Q. faginea* is the dominant tree in the overstory (38–51% cover), but it represents only a fraction (8–19%) of the recruits. In contrast, the arborescent shrub *V. tinus* has a small cover (5–10%) in the overstory canopy, but dominates in the regeneration layer (50–71%). This uncoupling of the community composition at adult and recruitment stages has been found in other Mediterranean forests (e.g., Pérez-Ramos and Marañón 2005) and indicates interspecies differences in the outcome of regeneration processes.

The disproportionate higher abundance of recruits of *V. tinus* in relation to the low density of adults for that species, as well as the predominant clumped spatial patterns for recruits of that species, can be explained by the high production of seeds and by their dispersal by birds below perches. They usually form a dense seedling bank in the understory (Pérez-Ramos 2007).

The arborescent shrub or small tree *A. unedo* had a regeneration potential that contrasted with that of *V. tinus*, showing relative high cover (34 and 38%) in the overstory canopy but relatively scarce recruitment (3 and 14%). Similar uncoupling of overstory-understory demography and limited regeneration of *A. unedo* has been documented for a mixed oak forest of southern Spain (Pérez-Ramos and Marañón 2005). The conspecific clumped pattern detected for recruits of *A. unedo* can be explained by fruits falling under the mother tree and by bird dispersion under the trees used as perches.

The conspecific spatial clumps identified for recruits of *Q. faginea* in the upper plot and recruits of *Q. suber* in the lower plot, i.e., where each species was less abundant in the overstory, can be explained by the dispersion of their seeds mainly by gravity near the mother tree or by the clumped

Table 3. Variance partitioning

	Plot U		Plot D	
	% total	% explained	% total	% explained
Total explained variance	37.7	100	25.6	100
Variance partition				
Spatially structured variance	29.3	78	20.3	79
Explained by environmental variables	6.5	17	6.2	24
Not explained by environmental variables	22.8	60	14.1	55
Nonspatially structured variance	8.4	22	5.3	21

sprouting. The higher abundance and recruitment success of the semideciduous oak (*Q. faginea*) in the lower plot agrees with other studies in Mediterranean mixed oak forests, where the semideciduous species tend to be more abundant in the lower slope and more fertile habitats (Benayas et al. 2005, Maltez-Mouro et al. 2005, Ajbilou et al. 2006). The denser, higher, and more complex canopy down-slope corresponds to more intense shade conditions and thus the recruits that are able to tolerate such low availability of light succeed there. The high abundance of the evergreen cork oak (*Q. suber*) in the upper slope forest, where it also shows a relatively good recruitment (28% of total recruits), contrasts with the lack of regeneration of cork oak found in other studies (e.g., Pérez-Ramos 2007). An important ecological factor in the forest studied is the low density of large herbivores (Alves and Ferreira 2004), which could explain the relatively successful recruitment. However, the low overstory abundance (5% and 19%) of cork oak and the many dead trees observed during the fieldwork suggest a progressive replacement of remnant old and injured (due to bark extraction) cork oaks by vigorous young semideciduous oaks; a similar replacement pattern was described in a mixed oak forest of North Morocco (Ajbilou et al. 2006).

Recruitment Spatial Patterns

The overall spatial pattern of recruits departed significantly from random, as has been found in most terrestrial ecosystems (Perry et al. 2002). Regarding the conspecific and interspecific patterns, there was as much evidence of CSR as of clumped patterns. Although CRS would be expected to occur by chance, some biotic or abiotic factors could have generated the identified clumps, and this applies to all patterns and not exclusively to strong ones (Grimm and Berger 2002).

It has been recognized that recruits of each species tend to clump within favorable microsites characterized by suitable microclimatic factors, depending on their physiological trade-offs and responses to microenvironmental filters (Holmgren et al. 1997, Holmgren 2000). Eventually, clumped patterns may turn into overdispersion due to competition for resources, but this would be expected only for larger-diameter classes (Skarpe 1991, Moeur 1993, Ward et al. 1996) and not at the studied phase of recruitment, when competition between individuals is comparatively weak.

The unexplained variance in the density of recruits (approximately 62 and 74% in plots U and D, respectively) could be due to some overlooked factors or to a large amount of stochastic variation (Borcard et al. 1992). However, an ordination diagram that explains a low percentage of variance of the data is quite informative (Gauch 1982), and therefore the spatial patterns detected with respect to the ordination diagrams in Figure 4 are discussed in the next section.

Factors Affecting Regeneration

The distance to the nearest conspecific adults (a major factor determining recruitment spatial patterns in both plots studied) reflects a dependence of recruits on their mother trees and dispersion strategies (Herrera et al. 1994, Jordano and Herrera 1995). Thus, some of the detected clumped patterns could be induced by vegetative propagation of recruits from roots (for *Quercus* species), and by dispersion under the mother tree (by gravity) or under trees used as perches by birds.

Both seedlings and vegetative recruits from roots tend to clump within favorable microsites characterized by suitable microclimatic factors. Light availability (indirectly measured as the inverse of canopy density) was an important factor in explaining the distribution of recruits and spatial associations of recruits in the plots studied. Optimal recruit densities were located in darker positions for shrubs (particularly for *A. unedo*) than for trees (*Quercus* species), suggesting that recruits of shade-tolerant shrubs were favored in sites having canopies with a closed shrub understory, whereas recruits of *Quercus* species reached their optima in sites under tree canopies and having a lower-density shrub understory. Higher soil moisture correlated positively with recruits of both *Quercus* species studied and negatively with recruits of *A. unedo.* However, soil moisture was a significant factor only in the upper plot, where the higher slope and lower litter accumulation directly or indirectly contribute to lower soil humidity, whereas the higher herbaceous ground cover has strong negative effects on the establishment of recruits due to competition for water (Benayas et al. 2005).

The lack of independence between species of recruits in the understory and species in the overstory and the importance of canopy density in explaining the variance in the density of recruits support the hypothesis that overstory structure and composition are important factors to explain the recruitment patterns. The overstory canopy promotes environmental changes underneath, modifying temperature, moisture, light quantity and quality, and litter quantity and quality (Maltez-Mouro et al. 2005, García et al. 2006) in comparison with open habitats. In fact, we found (in both studied plots) a positive association between increased litter depth and increased recruit density of *Q. faginea*, suggesting that recruits of the deciduous species are able to tolerate the deeper litter layers produced by the conspecific adults.

Importance of Spatial Component

Space may be considered either a main factor responsible for ecological structures, or a confounding one leading to bias (Dray et al. 2006). In both cases, the spatial component must be incorporated when one is analyzing ecological patterns to avoid spurious conclusions and to gain further insights on factors conditioning species distributions and community structure (Legendre 1993). In this case study, the spatial component was of major importance in explaining the distribution of recruits. Although environmental or canopy variables accounted for a considerable proportion (40–45%) of the explained variance in the density of recruits, the spatial distribution of recruits was also important in explaining the regeneration of different dominant species in the forest. A large proportion (55–60%) of the explained variance in the density of recruits was spatially structured

but not related to the measured environmental/canopy variables. This large "unidentified" source of spatially structured variance corresponds either to spatial patterns directly derived from contagious biotic processes at the community level or to community spatial patterns that have been induced by some unmeasured environmental variables that are spatially structured (Dray et al. 2006). Similar results have been found in other studies (Rubio and Escudero 2000, Maestre et al. 2003) related to woody species regeneration under Mediterranean conditions.

Literature Cited

AJBILOU, R., T. MARAÑÓ, AND J. ARROYO. 2006. Ecological and biogeographical analyses of Mediterranean forests of northern Morocco. *Acta Oecol.* 29(1):104–113.

ALVES, P.C., AND C. FERREIRA. 2004. *Determinação da abundância relativa das populações de coelho-bravo (Oryctolagus cuniculus algirus) em Portugal Continental. Protocolo de Colaboração no âmbito do projecto "Revisão do Livro Vermelho dos Vertebrados de Portugal.*" ICETA, Universidade do Porto, Portugal.

BADDELEY, A., AND R. TURNER. 2005. Spatstat: An R package for analyzing spatial point patterns. *J. Stat. Soft.* 12(6):1–42.

BADDELEY, A., M. KERSCHER, K. SCHLADITZ, AND B.T. SCOTT. 2000. Estimating the J function without edge correction. *Stat. Neerl.* 54(3):315–328.

BENAYAS, J.M.R., J. NAVARRO, T. ESPIGARES, J.M. NICOLAU, AND M.A. ZAVALA. 2005. Effects of artificial shading and weed mowing in reforestation of Mediterranean abandoned cropland with contrasting *Quercus* species. *For. Ecol. Manag.* 212:302–314.

BORCARD, D., AND P. LEGENDRE. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol. Model.* 153:51–68.

BORCARD, D., AND P. LEGENDRE. 2004. *Maker2—User's guide*. Département de sciences biologiques, Université de Montréal, Montréal, Quebec, Canada.

BORCARD, D., P. LEGENDRE, AND P. DRAPEAU. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73(3):1045–1055.

DI CASTRI, F., D.W. GOODALL, AND R.L. SPECHT. 1981. *Mediterranean-type shrublands.* Elsevier Scientific, Amsterdam, the Netherlands.

DIGGLE, P.J. 2003. *Statistical analysis of spatial point patterns*. Oxford University Press, New York. 159 p.

DOVCIAK, M., L.E. FRELICH, AND P.B. REICH. 2001. Discordance in spatial patterns of white pine (*Pinus strobus*) size-classes in a patchy near-boreal forest. *J. Ecol.* 89:280–291.

DRAY, S., P. LEGENDRE, P,-R. PERES-NETO. 2006. Spatial modelling: A comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Model.* 196:483–493.

FORTIN, M.J, AND M. DALE. 2005. *Spatial analysis—A guide for ecologists.* Cambridge University Press, Cambridge, United Kingdom. 365 p.

GARCÍA, D., AND G. HOULE. 2005. Fine-scale spatial patterns of recruitment in red oak (*Quercus rubra*): What matters most, abiotic or biotic factors? *Écoscience* 12:223–235.

GARCÍA, L.V. 2004. Escaping the Bonferroni iron claw in ecological studies. *Oikos* 105:657–663.

GAUCH, H.G. 1982. *Multivariate analysis in community ecology.* CambridgeUniversity Press, Cambridge, United Kingdom, 298 p.

GEORGE, L.O., AND F.A. BAZZAZ. 1999. The fern understorey as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology* 80(3):833–845.

GÓMEZ, J.M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography* 26:573–584.

GÓMEZ-APARICIO, L., F. VALLADARES, R. ZAMORA, AND J.L. QUERO. 2005. Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: An experimental approach at different scales. *Ecography* 28:757–758.

GOREAUD, F., AND R. PÉLISSIER. 2003. Avoiding misinterpretation of biotic interactions with the intertype K12-function: population independence vs. random labelling hypothesis. *J. Veg. Sci.* 14:681–692.

GRATZER, G., AND P.B. RAI. 2004. Density dependent mortality versus spatial segregation in early life stages of *Abies densa* and *Rhododendron hodgsonii* in Central Bhutan. *For. Ecol. Manag.* 192:143–159.

GRIMM, V., AND U. BERGER. 2002. Seeing the wood for the trees, and vice versa: Pattern-oriented ecological modeling. P. 411–428 in *Scales in aquatic systems: Measurement, analysis, simulation,* Seuront, L., and P.G. Strutton (eds.). Cooperative Research Center Press, Germany.

HERRERA, C.M., P. JORDANO, L. LÓPEZ-SORIA, AND J.A. AMAT. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecol. Monogr.* 64:315–344.

HOLMGREN, M. 2000. Combined effects of shade and drought on tulip poplar seedlings: Trade-offs in tolerance or facilitation? *Oikos* 90:67–78.

HOLMGREN, M., M. SCHEFFER, AND M.A. HUSTON. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78(7):1966–1975.

JORDANO, P., AND C.M. HERRERA. 1995. Shuffling the offspring: Uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Écoscience* 2(3):230–237.

MAESTRE, F.T., J. CORTINA, S. BAUTISTA, J. BELLOT, AND R. VALLEJO. 2003. Small-scale environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a semiarid degraded ecosystem. *Ecosystems* 6:630–643.

MAESTRE, F.T., A. ESCUDERO, I. MARTINEZ, C. GUERRERO, AND A. RUBIO. 2005. Does spatial pattern matter to ecosystem functioning? Insights from biological soil crusts. *Funct. Ecol.* 19:566–573.

MALTEZ-MOURO, S., L.V. GARCÍA, T. MARAÑÓN, AND H. FREITAS. 2005. The combined role of topography and overstory tree composition in promoting edaphic and floristic variation in a Mediterranean forest. *Ecol. Res.* 20:668–677.

MARAÑÓN, T., R. ZAMORA, R. VILLAR, M.A. ZAVALA, J.L. QUERO, I. PÉREZ-RAMOS, I. MENDOZA, AND J. CASTRO. 2004. Regeneration of tree species and restoration under contrasted Mediterranean habitats: Field and glasshouse experiments. *Int. J. Ecol. Envir. Sci.* 30:187–196.

MARCHAND, H. 1990. *Les forèts Méditerranéennes: Enjeux et perspectives. Les fascicules du Plan Bleu, 2*. Economica, Paris.

MILLER, T.F., D.J. MLADENOFF, AND M.K. CLAYTON. 2002. Old-growth northern hardwood forests: Spatial autocorrelation and patterns of understory vegetation. *Ecol. Monogr.* 72(4): 487–503.

MOEUR, M. 1993. Characterizing spatial patterns of trees using stem-mapped data. *For. Sci.* 39(4):756–775.

ØKLAND, R.H., AND O. EILERTSEN. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. *J. Veg. Sci.* 5:117–126.

PÉREZ-RAMOS, I.M. 2007. *Factores que condicionan la regeneración natural de especies leñosas en un bosque mediterráneo del*

sur de la Península Ibérica. Ph.D. dissertation, University of Seville, Seville, Spain.

PÉREZ-RAMOS, I.M., AND T. MARAÑÓN. 2005. Limitaciones en la regeneración natural de las especies leñosas de un bosque mediterráneo. *Almoraima* 31:129–135.

PERRY, J.N., A.M. LIEBHOLD., M.S. ROSENBERG, J. DUNGAN, M. MIRITI, A. JAKOMULSKA, AND S. CITRON-POUSTY. 2002. Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography* 25:578–600.

PNSACV. 2002. Plano Zonal Agro-Ambiental do Parque Natural do Sudoeste Alentejano e Costa Vicentina. In *Plano de Desenvolvimento Rural de Portugal Continental.* Portugal.

PULIDO, F.J., AND M. DÍAZ. Regeneration of a Mediterranean oak: A whole cycle approach. *Écoscience* 12(1):92–102, 2005.

R DEVELOPMENT CORE TEAM. 2006. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

RUBIO, A., AND A. ESCUDERO. 2000. Small-scale spatial soil-plant relationship in semi-arid gypsum environment. *Plant Soil* 220:139–150.

SACK, L., P.J. GRUBB, AND T. MARAÑÓN. 2003. The functional morphology of juvenile plants tolerant of strong summer drought in shaded forest understories in southern Spain. *Plant Ecol.* 168(1):139–163.

SEALY, J.R., AND D.A. WEBB. *Arbutus unedo* L. *J. Ecol.* 38:223–236, 1950.

SKARPE, C. 1991. Spatial patterns and dynamics of woody vegetation in an arid savanna. *J. Veg. Sci.* 2:565–572.

TER BRAAK, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179.

TER BRAAK, C., AND P. SMILAUER. 2002. *Canoco for Windows,* version 4.5. Center for Biometry Wageningen, Wageningen, the Netherlands.

THÖNNES, E., AND M.N.M. VAN LIESHOUT. 1999. A comparative study on the power of van Lieshout and Baddeley's J-function. *Biom. J.* 41:721–734.

VAN LIESHOUT, M.N.M. 2004. *A J-function for marked point patterns: Probability, networks and algorithms.* Report PNA-RO404. Amsterdam, the Netherlands.

VANDVIK, V., AND H.J.B. BIRKS. 2002. Partitioning floristic variance in Norwegian upland grasslands into within-site and between-site components: Are the patterns determined by environment or by land-use? *Plant Ecol.* 162:233–245.

WARD, J.S., G.R. PARKER., AND F.J. FERRANDINO. 1996. Long-term spatial dynamics in an old growth deciduous forest. *For. Ecol. Manag.* 83:189–202.